Neuropsychologia 112 (2018): 40-49

DOI: http://doi.org/10.1016/j.neuropsychologia.2018.02.027

Neural modulations of interference control over conscious perception

Itsaso Colás[a], Almudena Capilla[b], Ana B. Chica[a]

[a] Centro de Investigación Mente, Cerebro y Comportamiento (CIMCYC), Departamento de Psicología Experimental, Universidad de Granada, Granada, Spain.

[b] Departamento de Psicología Biológica y de la Salud, Universidad Autónoma de Madrid, Madrid, Spain.

Itsaso Colás (corresponding author)
icolas@ugr.es
Almudena Capilla
almudena.capilla@uam.es
Ana B. Chica (corresponding author)
anachica@ugr.es

Abstract

The relation between attention and consciousness is a highly debated topic in Cognitive Neuroscience. Although there is an agreement about their relationship at the functional level, there is still no consensus about how these two cognitive processes interact at the neural level. According to the gateway hypothesis (Posner, 1994), attention filters the information accessing to consciousness, resulting in both neural and functional modulations. Contrary to this idea, the cumulative influence hypothesis (Tallon-Baudry, 2012) proposes that both attention and consciousness independently impact decision processes about the perception of stimuli. Accordingly, we could observe an interaction between attention and consciousness at the behavioral level, but not at the neural level. Previous studies have shown that alerting and orienting networks of attention modulate participants' ability to verbally report near-threshold visual stimuli both at behavioral and neural levels, supporting the gateway hypothesis over the cumulative influence hypothesis. The impact of the executive control network of attention on conscious perception, however, has only been explored behaviorally (Colás et al., 2017). In the present study, we employed high-density encephalography to investigate the neural basis of the interaction between executive attention and conscious perception. We presented a classical Stroop task concurrently with a detection task of near-threshold stimuli. In two

separate sessions, we manipulated the proportion of congruent and incongruent Stroop stimuli. We found that the Stroop-evoked N2 potential (usually associated to conflict detection and localized in the anterior cingulate cortex) was modulated by both conflict detection and conscious perception processes. These results suggest that the relation between executive control and conscious perception lies in frontal lobe regions associated to conflict detection, supporting the gateway hypothesis over the cumulative influence hypothesis.

Highlitghts:

- Executive control and consciousness interact at the behavioral and neural level.
- The conflict-related N2 component discriminates between seen and unseen targets.
- The N2 component was associated to activation of the anterior cingulate cortex.

Keywords: executive control; conscious perception; proactive and reactive control; proportion congruent; ERP; source localization.

1. Introduction

We can only report a small portion of the information reaching our senses, but how this information is selected is still an open question in Cognitive Neuroscience. Attention has been proposed as the selection mechanism that filters the access of visual information into consciousness (Bartolomeo, 2008; Dehaene et al., 2006; Dehaene and Naccache, 2001; Posner, 1994). Dehaene and colleagues (Dehaene et al., 2006, 2003; Dehaene and Changeux, 2004; Dehaene and Naccache, 2001) suggest that the extent to which a certain stimulus gains access to conscious processing depends not only on (bottom-up) stimulus strength but also on top-down attentional amplification. This idea follows the Global Neuronal Workspace model (Baars, 2005, 2002) of conscious access, which states that to be consciously perceived (and therefore accessible to higher order cognitive functions such as memory, language, and action-planning) the neural representation of sensory information has to propagate to distributed large-scale networks in the global neuronal workspace. The model emphasizes the hierarchical organization of the brain, separating lower automatized and specialized systems from the supervisory executive system (Dehaene and Changeux, 2004). Other models also highlight the importance of attentional amplification for conscious perception (Petersen and Posner, 2012; Posner and Petersen, 1990), proposing attention as the gateway to consciousness.

The use of neuroimaging techniques in paradigms comparing conscious and unconscious processing of information has identified some key nodes in the frontal and parietal cortices that seem to be critically involved in conscious perception (for reviews, see Aru et al., 2012; Chica and Bartolomeo, 2012; De Graaf et al., 2012; Dehaene and Changeux, 2011). Given that the neural ignition of long-distance networks in the brain appears crucial for conscious perception, we could assume that changes in brain activity preceding the presentation of information also play an important role in conscious processing. In fact, existing evidence corroborates that conscious access can be predicted by pre-stimulus activation (Mathewson et al., 2009; Wyart and Tallon-Baudry, 2009). Accordingly, fluctuations in attention before stimulus presentation should modulate conscious perception.

The relation between attention and conscious perception has already been explored in the literature. Based on Petersen and Posner's theoretical model (Petersen and Posner, 2012; Posner and Petersen, 1990), attention can be divided into three functionally and anatomically distinct networks: alertness, orienting, and executive control. Behavioral studies have

demonstrated that phasic alertness and exogenous spatial attention improve the conscious perception of visual stimuli (Chica et al., 2012, 2011; Kusnir et al., 2011; Petersen et al., 2017). However, interactions between both attentional systems and conscious perception occur through segregated brain networks. The interaction between phasic alerting and conscious perception is mediated through a fronto-striatal network including the anterior cingulate cortex, the supplementary motor area, the caudate, and the frontal eye-fields (Chica et al., 2016). The interaction between spatial attention and conscious perception is instead associated to the activity of the left frontal eye field, the bilateral superior and inferior parietal lobes, and the right inferior frontal gyrus (Chica et al., 2013).

Recently, interference control was demonstrated to modulate the conscious perception of near-threshold stimuli, making participants' decision criterion more conservative after incongruent as compared to congruent Stroop trials (Colás et al., 2017). Interference control is one of the three core components of executive function, that could be equivalent to executive control, as it enables us to attend selectively, focusing on some features or stimuli while suppressing attention to others (Diamond, 2013; Petersen and Posner, 2012). The present study addresses for the first time the neural mechanisms underlying the modulation of conscious perception by interference control. According to the cumulative influence hypothesis (Tallon-Baudry, 2012), the frontal lobes play an key role on the decisional stage of verbally reporting consciously perceived information. It is proposed that the information of attentional and perceptual systems is analyzed in different and independent brain networks, being integrated within the frontal lobe for decision-making (decision about reporting the stimulus presence or absence). Contrary, both the Global Neural Workspace model (Baars, 2005, 2002; Dehaene et al., 2006) and the gateway hypothesis (Petersen and Posner, 2012; Posner, 1994) state that attentional amplification should modulate conscious access in the prefrontal-parietal network. Therefore, attentional recruitments in conflict trials should result in a neural interaction (likely in frontal regions) between interference control and conscious perception.

We conducted an electroencephalography (EEG) study adapting the paradigm used in Colás et al. (2017), which combined a typical Stroop-task (with congruent and incongruent stimuli) with a conscious detection task of near-threshold stimuli (in which stimuli were individually titrated to achieve ~50% consciously reported Gabors). Both tasks were presented in a concurrent manner, so that trials could be sorted into congruent-seen,

congruent-unseen, incongruent-seen, and incongruent-unseen. Participants conducted two separate sessions; in one of them, 75% of the Stroop trials were congruent and 25% of the trials were incongruent, a manipulation known to prompt reactive control due to the low expectancy of interference (Botvinick et al., 2001; Braver, 2012; De Pisapia and Braver, 2006). In the other session, 25% of the Stroop trials were congruent and 75% of the trials were incongruent, increasing the recruitment of proactive control as a consequence of the high expectancy of interference (Botvinick et al., 2001; Braver, 2012; De Pisapia and Braver, 2006). Following the dual mechanisms framework of control (Braver, 2012; De Pisapia and Braver, 2006), individuals can either rely on a reactive strategy of cognitive control, activated only after conflict detection, or employ a proactive control strategy which is maintained through the block of trials. The recruitment of these two mechanisms of control can depend on task contingencies or individual differences, or can just wax and wane spontaneously during a block of trials (Kalanthroff et al., 2014).

We analyzed the anterior N2 component locked to the appearance of the Stroop word, a component that has been related to conflict solving (Folstein and Van Petten, 2008; Luck, 2012). We expected an overall enhanced N2 component when the Stroop word was incongruent as compared to congruent trials, due to interference control recruitment. We hypothesized that this difference would be larger when participants had to implement reactive control (on incongruent trials from the high proportion congruent session), because according to the dual mechanisms framework (Braver, 2012; De Pisapia and Braver, 2006), proactive control would be maintained across both congruent and incongruent trials in the low proportion congruent session. In addition, we conducted source-localization analyses, and we expected the N2 component to be localized in the anterior cingulate cortex (Van Veen and Carter, 2002). Moreover, if the interaction between interference control and conscious access was supported at the neural level, the N2 component should differentiate between consciously perceived and non-perceived near-threshold stimuli. We hypothesized an interaction between interference control and conscious perception, expecting a larger N2 component for incongruent seen as compared to incongruent unseen trials, especially in the high proportion congruent session. Results from this study will show for the first time the when and where of the neural basis of the interaction between interference control and the conscious perception of near-threshold stimuli.

2. Methods

2.1. Participants

Twenty-six students from the University of Granada (Spain) gave their signed informed consent to participate in the study in exchange of course credit. Five participants did not attend the second session of the study and were removed from the analyses. Therefore, data from twenty-one participants (3 men; mean age of 21 years, SD = 3.69) were included for the behavioral analyses. For the ERP analyses, data from four further participants were excluded because, after applying artifact detection tools, they had less than 15 trials per condition. The study was approved by the Human Ethical Committee from the University of Granada, in compliance with the ethical standards of the 1964 Declaration of Helsinki.

2.2. Apparatus and stimuli

E-prime software (Schneider et al., 2002) was used for the presentation of stimuli and behavioral data collection. Experiments were conducted using a 17" DELL monitor running at 85Hz. Participants sat at approximately 57 cm from the screen. Two black markers and a centered fixation point (a black plus sign, 0.3° × 0.3°) were displayed at the beginning of each trial. The markers consisted of a black square outline (6° width × 4.5° height), placed 8° to either the left or the right side of the fixation point (distance measured from the center of the fixation point to the center of the lateral marker). Spanish words for blue (*azul*, 1.5° × 0.5°), green (*verde*, 2° × 0.5°), and yellow (*amarillo*, 4° × 0.5°) colors were presented 1° above fixation. Words were presented either in blue, green, or yellow ink, and could make a given trial congruent (when word meaning and ink color matched) or incongruent (when word meaning and ink color did not match). Inside the lateral markers, a *Gabor* stimulus could appear. Matlab 8.1. (http://www.mathworks.com) was used to create 100 Gabor stimuli (4 cycles/deg. spatial frequency, 2.5° in diameter, SD of 0.3°), with a maximum and minimum Michelson contrast of 0.92 and 0.02, respectively.

2.3. Procedure

Figure 1 shows the timing and sequence of events in a given experimental trial. The duration of the fixation display varied randomly between 1008 and 1752 ms. The Stroop word was then presented for 492 ms, and the Gabor stimulus (lasting 36 ms) appeared 252 ms after the word onset. Participants could respond to the Stroop word from the moment it was displayed and for a maximum period of 2016 ms (word duration plus 1524 ms). After that,

participants were required to respond to the Gabor detection task, with no time limit. An inter-stimulus interval of 2508 ms was set after the Gabor response, allowing participants to blink and prepare for the next trial.

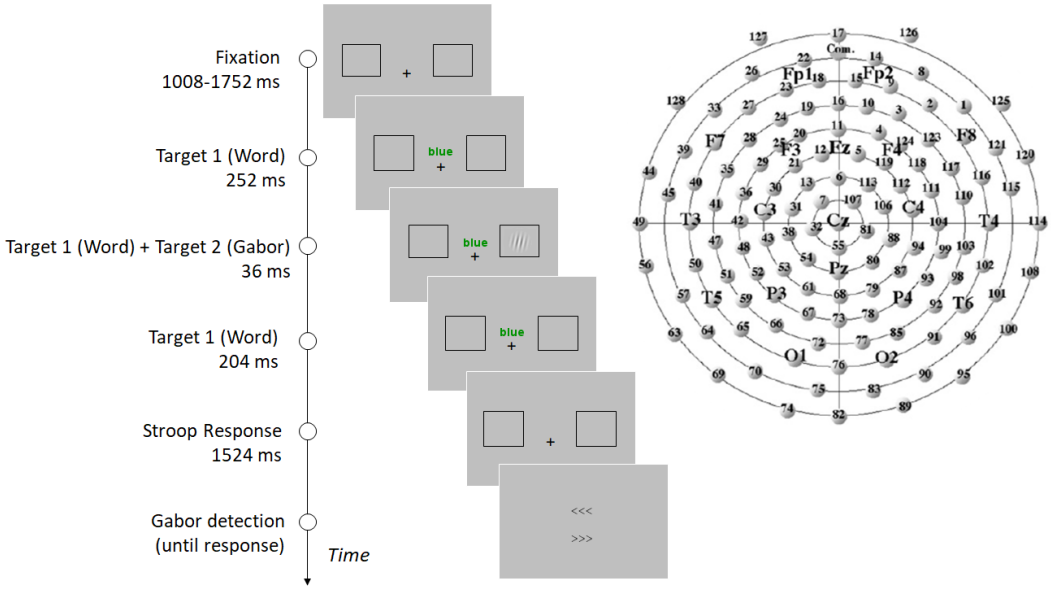


Figure 1. Timing and sequence of events in a given experimental trial (left). Electrode distribution around the scalp (right; the top of the figure represents the frontal area). Additional sites according to the 10–20 international system are shown for further reference.

Participants were required to perform two consecutive tasks. First, they had to discriminate the word's ink color as fast and accurately as possible. Participants responded with their right hand, pressing a keyboard key for each given color (the color-key mapping was counterbalanced across participants). On 12% of the trials no word was presented and no response was required. Then, participants performed the Gabor detection task, reporting if they had perceived its appearance. They were asked to respond accurately and without time pressure, reporting the Gabor location only when they were confident about their perception. The response was given by choosing one of two arrow-like stimuli (>>> or <<<), pointing to the two possible locations of the Gabor: right and left sides of the screen. The arrows were presented one above the other, with their position randomized in each trial. Participants indicated the location of the Gabor with their left hand, pressing an upper keyboard key corresponding to the upper arrow, or a lower key corresponding to the bottom arrow. This response procedure was employed in order to minimize response preparation and anticipations (Chica et al., 2011). Participants were asked to press the space bar whenever

they had not perceived the stimulus. No Gabor was presented on 19% of the trials (catch trials).

Before the experimental trials, participants passed through a titration procedure, where Gabor contrast was calibrated for each participant in the absence of the Stroop stimulus. During titration, participants had to detect the Gabor and select its location. Titration began with a supra-threshold stimulus (Michelson contrast = 0.184), which contrast was manipulated based on the mean percentage of seen Gabors every 16 trials. If participants reported 63% or more Gabors during the last block of trials, Gabors at the immediately following lower contrast level (Michelson contrast minus 0.009) were used during the next block of trials; however, if the percentage of seen Gabors was equal or lower than 38% during the last block of trials, the next block of trials presented Gabors at the immediately following higher contrast level (Michelson contrast plus 0.009). The titration procedure stopped when Gabor contrast yielded a percentage of seen targets >38% and <63% for two consecutive blocks of 16 trials.

Participants completed two separate sessions, each containing titration, practice (15 trials), and experimental trials. In one of the sessions, congruent trials were more frequent than incongruent trials (75% congruent trials - 25% incongruent trials; high proportion congruent session), whereas in the other session, incongruent trials were more frequent than congruent trials (75% incongruent trials - 25% congruent trials; low proportion congruent session). The order of the sessions was counterbalanced across participants. The experiment consisted of a total of 1088 experimental trials (544 trials per session, divided in 4 experimental blocks of 136 trials). Therefore, a total of 360 congruent trials and 120 incongruent trials were presented in the high proportion congruent session (no Stroop word was presented in the remaining 64 trials). In the low proportion congruent session, the proportion of congruent and incongruent trials reversed, giving a total of 360 incongruent trials, 120 congruent trials, and 64 trials in which the word was not presented. Each session contained a total of 96 Gabor catch trials (trials in which the Stroop word was presented in absence of the Gabor stimulus). Participants were allowed to take a short break after every 68 trials. Additionally, after every 136 trials, the experimenter checked the impedance of the electrodes to try and keep it below 50 KΩ.

220 2.4. EEG signal recording and analysis

221 The analysis of the EEG signal at the sensor level was performed using the Net Station
222 software package (https://egi.com/). After preprocessing the EEG signal, event-related
223 potentials locked to the Stroop word were analyzed.

224 Source-level analysis was performed using the FieldTrip software package
225 (Oostenveld et al., 2011; http://www.ru.nl/fcdonders/fieldtrip/) and in-house Matlab code. Its
226 aim was to identify the neural generators underlying the N2 component modulations.

227 2.4.1. Sensor level analysis

228 EEG was recorded using a high-density 128-channel Geodesic Sensor Net (Tucker et
229 al., 1994; see Figure 1). The head-coverage included sensors lateral to and below both eyes to
230 monitor horizontal and vertical eye movements (HEOG and VEOG). Impedances for each
231 channel were measured and kept below 50 KΩ before testing. All electrodes were referenced
232 to the Cz electrode during recording and were re-referenced to the average of all electrodes
233 off-line. The EEG signal was acquired at a sampling rate of 250 Hz. It was band-pass filtered
234 online between 0.1 and 100 Hz using an elliptic filter, and subsequently filtered offline by
235 using a 0.3–30 Hz band-pass Butterworth filter. Epochs were segmented from 200 ms before
236 the presentation of the Stroop word to 450 ms after its appearance. A 200 ms segment prior to
237 the Stroop word presentation was used to calculate the baseline. Trials containing eye blinks
238 or eye movements (electro-oculogram channel differences greater than 70 μV) or trials with
239 more than 20% of bad channels were rejected. Overall, a total of 22% of the trials were
240 rejected due to artifacts or to anticipatory responses. Data from four participants were
241 excluded because after applying artifact detection tools, less than 15 trials per condition
242 remained. Word-related ERP analyses were performed over the following mean total of trials:
243 for the high proportion congruent session, congruent-seen (137), congruent-unseen (94),
244 incongruent-seen (40) and incongruent-unseen (29); for the low proportion congruent session,
245 congruent-seen (44), congruent-unseen (35), incongruent-seen (125) and incongruent-unseen
246 (109).

247 2.1.2. Source level analysis

248 The localization of brain sources was carried out by means of beamforming (Gross et
249 al., 2001; Van Veen et al., 1997). Source localization was performed on a standard MRI in

MNI (Montreal Neurological Institute) space provided by the EEGLAB toolbox (https://sccn.ucsd.edu/eeglab/), which was segmented into 12-mm resolution voxels. The forward model was computed using a standard boundary element method (BEM) volume conduction model (Oostenveld et al., 2003) and standard electrode positions. Lead fields were calculated for the 3 possible orientations of each voxel. We computed the spatial filter coefficients by means of linearly constrained minimum variance beamformer (LCMV; Van Veen et al., 1997). In order to obtain the filter coefficients, the single-trial covariance matrix was calculated for 444 ms segments corresponding to the time window after the Stroop word presentation, as well as 200 ms from the baseline period. Regularization (lambda parameter) was set to 10%, i.e. a unit matrix scaled to 10% of the mean across eigenvalues of the covariance matrix was added to it. Subsequently, each sensor-level trial was projected into each voxel of source-space through the spatial filter corresponding to the optimally oriented dipole. Source-level trials were averaged for the different conditions separately, thus obtaining the corresponding source-level ERPs. To avoid differences in amplitude due to voxels depth, source-level ERPs were all normalized as relative change with respect to the root mean square of the baseline activity for each voxel (Capilla et al., 2013). Finally, we averaged the brain activation results across subjects and identified the voxels exhibiting absolute spatial maxima/minima in the time window of the ERP component of interest (i.e. N2 component).

3. Results

3.1. Behavioral results

Data from twenty-one participants were included in the behavioral analyses. Participants perceived an average of 54% of the trials (SD= 13%). The mean rate of false alarms was 4.1% (SD= 6.4%). Mean Gabor contrast (averaged contrast levels used during the experiment for each participant) was not different in the high proportion congruent session and the low proportion congruent session, $t(20)= -0.05$, $p=.95$.

We firstly analyzed mean accuracy and reaction times (RTs) to respond to the Stroop task. We performed two independent analyses of variance (ANOVA), with the within participants factors of proportion congruency (high proportion congruent and low proportion congruent sessions), congruency (congruent and incongruent Stroop trials), and awareness (near-threshold Gabors reported as “seen” or “unseen”).

Second, we analyzed responses to the Gabor detection task to explore participants' conscious perception of the Gabor and its modulation by interference control. We analyzed participants' responses by using the signal detection theory, which provides a measure of perceptual sensitivity (d') and response criterion (beta). The indexes were calculated by computing participants' hits or correct detections (when participants accurately determined the location of a presented Gabor, i.e. "seen" Gabors), misses (trials in which the Gabor was presented but participants did not consciously report it, i.e. "unseen" Gabors), false alarms (when participants consciously reported Gabors that were not presented), and correct rejections (trials in which the Gabor was not presented and participants reported not having seen it). Trials in which participants incorrectly reported the location of a present Gabor were considered errors and removed from the analyses (1.83% of presented Gabors). Trials in which participants pressed any key before the presentation of the Gabor detection response display were considered anticipations and removed from the analyses (0.22% of the trials in which Gabors were presented). Trials in which participants committed an error in the Stroop task were also excluded from the Gabor detection task analyses (9.77% of the remaining trials). After eliminating Gabor detection errors and Stroop trial errors, a mean of 947 trials (SD=66) per participant were included in the analyses.

Perceptual sensitivity (d') and response criterion (beta) were calculated with the following equations: $d' = z(H) - z(FA)$; $\beta = Yz(H)/Yz(FA)$. H represents the hit rate, FA represents the false alarm rate, and z corresponds to z-scores, which were calculated using the inverse cumulative distribution function in Microsoft Excel 2011 (NORMSINV). The Y-score corresponds to the normal distribution function in Microsoft Excel 2011. Zero false alarm rates were corrected using the equation proposed by Snodgrass and Corwin (1988): $FA = (FA + 0.5)/(FA + CR + 1)$. For d', larger values indicate an increased perceptual sensitivity (more hits and/or less false alarms). Beta = 1 indicates a non-biased criterion; the higher the beta value, the more conservative the criterion (fewer hits and/or fewer false alarms), and the smaller the beta value, the less conservative the criterion (more hits and/or more false alarms).

Mean d' and beta indexes were submitted to two repeated measures ANOVAs with the within participants factors of proportion congruency (high and low proportion congruent) and congruency (congruent and incongruent). For all analyses, post-hoc Fisher tests were used to further explore the interactions.

3.1.1 Stroop task

The analysis of the mean RTs demonstrated a main effect of congruency, $F(1, 20)=53.06$, $p<.001$, $\eta_p^2 =.73$, with shorter RTs for congruent than for incongruent trials (see Table 1). As expected, this congruency effect was modulated by proportion congruency, $F(1, 20)=34.43$, $p<.001$, $\eta_p^2 =.63$. Although the congruency effect was significant for both sessions (both *p*s < .001), the effect was larger in the high proportion congruent session as compared with the low proportion congruent session. None of the other main effects or interactions were significant (all *p*s >.10).

Table 1. Mean RTs (in ms) and accuracy in the Stroop task, with standard errors in parenthesis, as a function of proportion congruency (high and low proportion congruent session), congruency (congruent and incongruent trial), and awareness (Gabors reported as "seen" or "unseen").

	High proportion congruent 75% congruent – 25% incongruent				**Low proportion congruent 25% congruent – 75% incongruent**			
	Congruent trial		**Incongruent trial**		**Congruent trial**		**Incongruent trial**	
	Seen	**Unseen**	**Seen**	**Unseen**	**Seen**	**Unseen**	**Seen**	**Unseen**
Mean RT	649 (35)	639 (27)	768 (53)	771 (39)	617 (31)	619 (28)	663 (31)	663 (27)
Mean accuracy	.93 (.02)	.92 (.02)	.85 (.03)	.81 (03)	.93 (.02)	.89 (.02)	.89 (.02)	.87 (.02)

The analysis of the mean accuracy in the Stroop task demonstrated a main effect of congruency, $F(1, 20)=29.85$, $p<.001$, $\eta_p^2 =.60$, which significantly interacted with proportion congruency, $F(1, 20)=9.88$, $p=.005$, $\eta_p^2 =.33$. Participants were more accurate in congruent trials as compared with incongruent trials in the high proportion congruent session ($p<.001$). In the low proportion congruent session, the congruency effect did not reach significance (Fisher post-hoc test, $p=.07$). A main effect of awareness was also observed, $F(1, 20)=14.61$, $p=.001$, $\eta_p^2 =.42$, demonstrating that participants were more accurate in the Stroop task in trials where they also perceived the Gabor stimulus as compared with trials in which the Gabor was missed (see Table 1). None of the other main effects or interactions reached statistical significance (all *p*s >.10).

3.1.2 Gabor detection task

The interaction between proportion congruency and congruency was not significant for the d' index, $F(1, 20)=2.56$, $p=.12$, $\eta_p^2 =.11$, but it reached statistical significance for the beta index, $F(1, 20)=9.14$, $p=.007$, $\eta_p^2 =.31$. Response criterion was comparable for incongruent trials in the high and low proportion congruent sessions ($p=.478$), while a more conservative criterion was observed for congruent trials in the low proportion congruent session as compared with the high proportion congruent session ($p<.001$) (see Table 2). Within the low proportion congruent session, response criterion to detect the Gabor was more conservative for congruent trials as compared with incongruent trials ($p=.014$). The reversed pattern was observed in the high proportion congruent session, although it did not reach statistical significance ($p=.131$). No other main effects or interactions reached statistical significance (all ps >.08 for d', and all ps >.21 for beta).

Table 2. Mean percentage of hits, false alarms, d', and beta to detect the near-threshold Gabor (with standard errors in parenthesis), as a function of proportion congruency (high and low proportion congruent session) and congruency (congruent and incongruent trial).

	High proportion congruent 75% congruent – 25% incongruent		**Low proportion congruent 25% congruent – 75% incongruent**	
	Congruent trial	**Incongruent trial**	**Congruent trial**	**Incongruent trial**
Mean hits	.57 (.03)	.56 (.03)	.55 (.03)	.53 (.03)
Mean FA	.05 (.02)	.06 (.02)	.03 (.02)	.03 (.01)
Mean d'	2.14 (.17)	2.13 (.20)	2.42 (.18)	2.18 (.16)
Mean beta	10.22 (1.75)	13.53 (2.34)	20.72 (2.02)	15.05 (2.34)

3.2. EEG results

Seventeen participants were included in the EEG analyses. Behavioral results from these participants showed the same main effects and interactions as the results described above.

We analyzed the event-related potentials (ERPs) locked to the appearance of the Stroop word. Within each session (high proportion congruent and low proportion congruent), we set up 4 conditions based on congruency of the Stroop word (congruent and incongruent Stroop trials) and awareness of the Gabor (targets reported as "seen" or "unseen"). Visual inspection of Stroop-related ERPs in both sessions revealed three main components (see Figure 2). We firstly observed a P1 component (peaking at 120 ms) in parieto-occipital

electrodes. This component was followed by a left lateralized parieto-occipital negativity, the N1 component (peaking at 190 ms). Finally, we observed a negative N2 component in left-lateralized frontal electrodes, peaking at 320 ms.

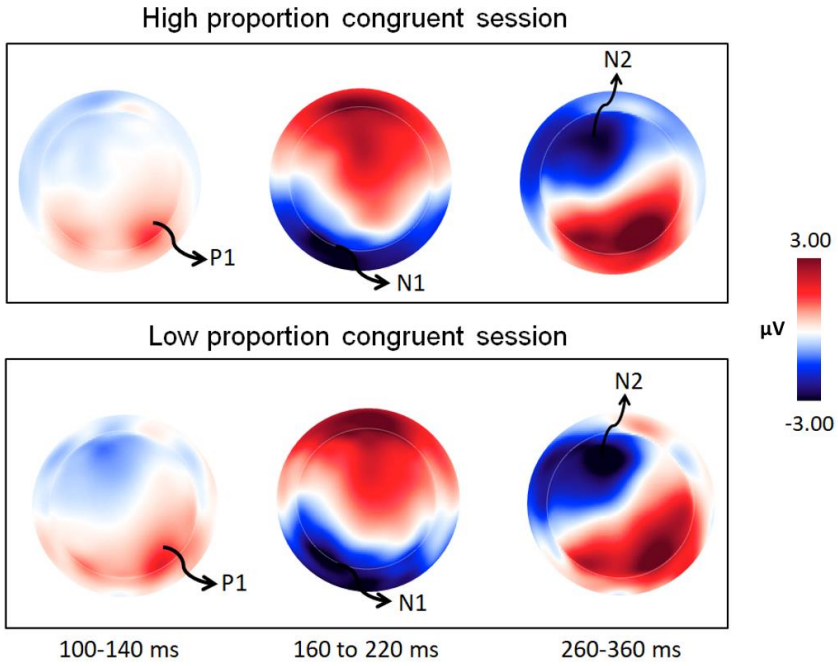


Figure 2. Topography maps for components P1, N1, and N2 for the high proportion congruent session (upper panel) and the low proportion congruent session (lower panel).

We calculated the mean amplitude of P1 (time window from 100 to 140 ms after the Stroop word onset), N1 (time window from 160 to 220 ms), and N2 (time window from 260 to 360 ms) for each participant in a sample of representative electrodes from the 10-20 electrode system (O1/O2, P3/P4, T5/T6, Pz, T3/T4, C3/C4, electrodes 21/25 representing F3 and electrodes 119/124 representing F4, electrodes 11/12/5 representing Fz, F7/F8) (see Chica et al., 2012). To determine the scalp location where each component was maximally elicited, we performed a one-way ANOVA for each component, with electrode as a factor. For all components, the main effect of electrode was significant (all *p*s < .05). The P1 component was larger in P3/P4 electrodes (M= .88 µ), followed by the Pz electrode (M= .34 µ). These two amplitudes were statistically different (post-hoc planned comparisons, $p = .01$), therefore, we only included electrodes P3 and P4 in the P1 analysis. The largest mean amplitude of the N1 component was observed in electrodes O1/O2 (M= −1.61 µ), followed by electrode T5 (M= −1.60 µ). These two amplitudes did not differ statistically (post-hoc planned comparisons, $p = .99$). The N2 component was larger in Fz electrode (M= -2.16 µ), followed

by left-lateralized electrodes F3 (M= -2.03 μ) and F7 (M= -1.92 μ). These amplitudes did not differ statistically (Fisher post-hoc test, all *p*s > .64). T3 amplitude did not differ from the Fz, F7and F3 electrodes, but this electrode was not included in the analysis because the anterior N2 component (sensitive to the violation of expectations and conflict detection) has been associated to frontal and central electrodes rather than to temporal electrodes (Folstein and Van Petten, 2008; Luck, 2012).

3.2.1 Mean amplitude analyses

We analyzed the modulation of each component for each experimental condition by calculating its mean amplitude (20 ms before and 20 ms after the higher peak) at the electrodes where each component was maximally elicited (P3/P4 electrodes for the P1 component, electrodes O1/O2 and T5 for the N1 component, and electrodes F3, F7, and Fz for the N2 component).

The ANOVAs for the P1 and N1 components, with the factors of proportion congruency, congruency, and awareness, did not show any significant main effects or interactions (all *p*s > .10).

For the N2 ANOVA, a main effect of awareness was observed, $F(1,16)= 7.30$, $p = .016$, $\eta_p^2 = .31$. N2 was enhanced for seen as compared with unseen trials. This effect was mediated by an interaction between proportion congruency, congruency, and awareness, $F(1,16)= 11.17$, $p = .004$, $\eta_p^2 = .41$ (see Figure 3). In the high proportion congruent session, incongruent trials elicited a larger N2 for seen as compared with unseen trials (Fisher post-hoc test, $p=.04$). Although not significant, the effect reversed for congruent trials ($p=.13$). In the low proportion congruent session, by contrast, seen trials elicited an overall larger N2 component than unseen trials, although the effect was only significant for congruent trials ($p=.001$; $p=.35$ for incongruent trials).

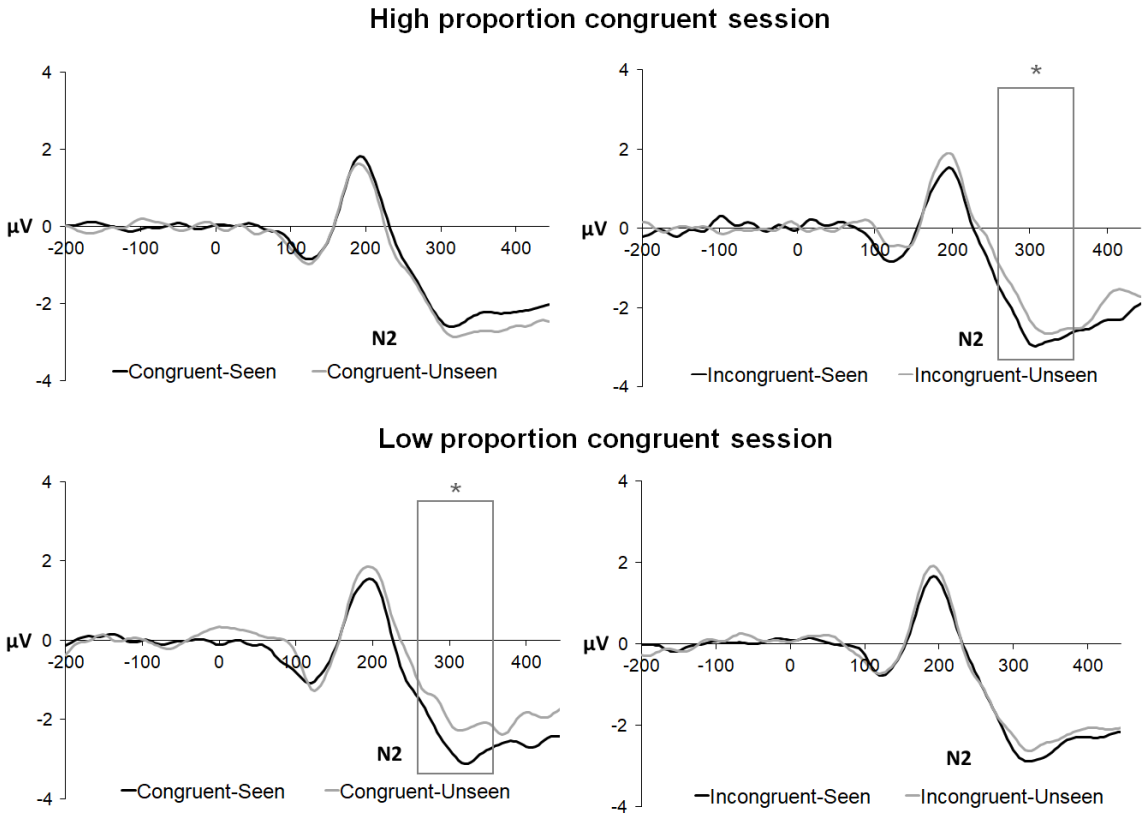


Figure 3. N2 component amplitude for electrodes F3, F7, and Fz as a function of congruency and awareness for the high proportion congruent session and the low proportion congruent session. The y-axis represents the amplitude of the wave (in μV). The x-axis represents time, with the value 0 corresponding to the onset of the Stroop word. In the high proportion congruent session, N2 amplitude was enhanced for incongruent seen trials as compared with incongruent unseen trials. In the low proportion congruent session, N2 amplitude was enhanced for seen as compared to unseen trials for both congruency conditions, although the effect only reached significance for congruent trials.

3.2.2 Source-location analyses

We first compared the neural sources underlying the N2 component for congruent and incongruent trials in the high proportion congruent and the low proportion congruent sessions (see Figure 4). Overall, the anterior cingulate cortex (ACC), which has been related to conflict detection and conflict monitoring (Botvinick et al., 2004, 2001; Carter et al., 1999), showed more activation for incongruent as compared to congruent Stroop trials. While the activation of the ACC was observed for incongruent trials but not for congruent trials in the high proportion congruent session, the ACC was activated for both incongruent and congruent trials in the low proportion congruent session. This observation is in agreement with the dual mechanisms of control framework (Braver, 2012; De Pisapia and Braver, 2006).

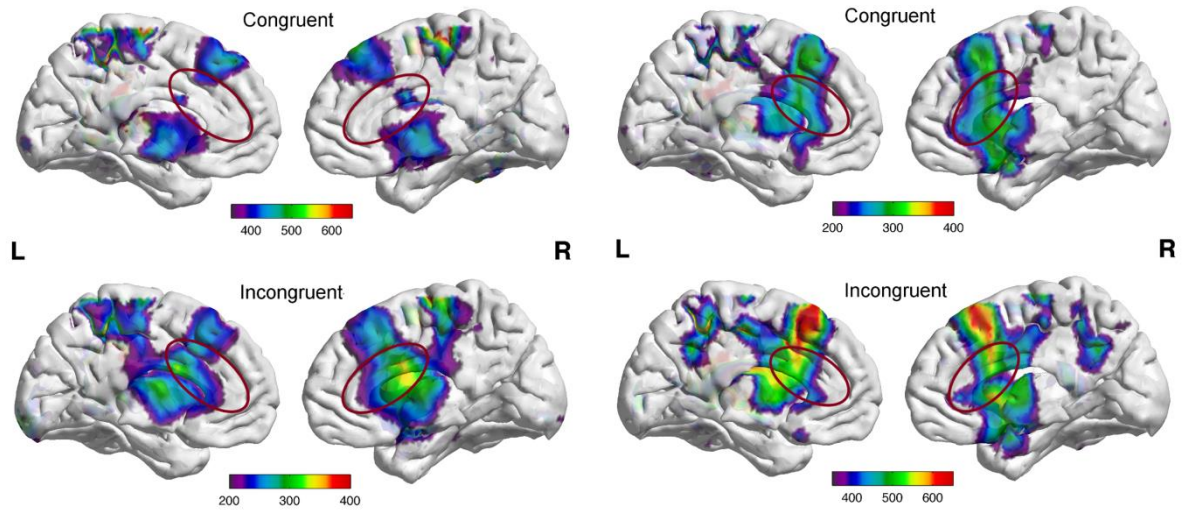
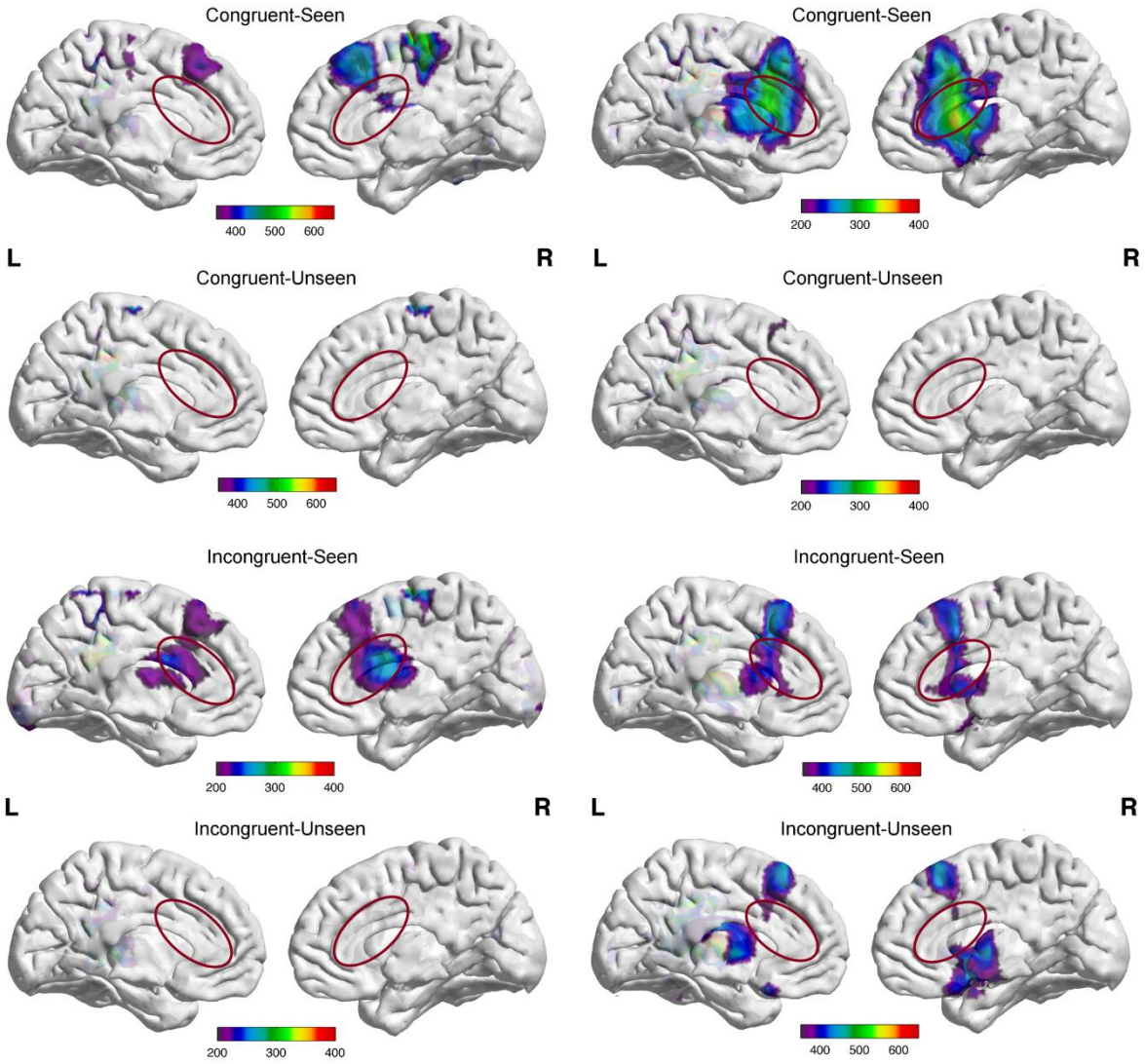


Figure 4. Medial view of the brain sources with maximum percent relative change in activation for the N2 component. Greater values (and/or warmer colors) represent greater brain activity in those areas during the N2 time window, expressed as percent relative change respect to the baseline (pre-stimulus) period. Left panel shows the brain sources for the N2 component for the high proportion congruent session, whereas right panel shows the brain sources for the low proportion congruent session. Congruent trials are represented in the upper panel and incongruent trials in the bottom panel. The red ellipse indicates the location of the anterior cingulate cortex (ACC).

We then observed the activation of the ACC as a function of awareness, congruency, and proportion congruency (see Figure 5). In the high proportion congruent session, the ACC was activated for seen but not for unseen Gabors, but only when trials were incongruent. In the low proportion congruent session, the ACC was activated for seen but not for unseen Gabors both on congruent and incongruent trials.



433

434 **Figure 5.** Medial view of the brain sources with maximum percent relative change in activation for the N2
435 component in the high proportion congruent session (left) and the low proportion congruent session (right) as a
436 function of congruency and awareness. Greater values (and/or warmer colors) represent greater brain activity in
437 those areas during the N2 time window, expressed as percent relative change respect to the baseline (pre-
438 stimulus) period. The red ellipse indicates the location of the anterior cingulate cortex (ACC).

439 **4. Discussion**

440 The present study addressed for the first time the neural mechanisms underlying the
441 interference control modulation of conscious perception. We explored whether the behavioral
442 interaction between interference control and conscious perception found in Colás et al. (2017)
443 reflected a neural interaction in the N2 component, associated to conflict resolution (the
444 anterior N2 component, Folstein and Van Petten, 2008; Luck, 2012), usually localized in

fronto-central electrodes and corresponding to neural activity in the ACC (Van Veen and Carter, 2002). The finding of this interaction is hypothesized by the attentional gateway hypothesis (Petersen and Posner, 2012; Posner, 1994), while the cumulative influence hypothesis (Tallon-Baudry, 2012) predicts that interference control and conscious perception mechanisms could be dissociated at the neural level.

The experimental paradigm employed allowed us to manipulate interference control as a mental task-set, prompting the recruitment of either reactive or proactive control mechanisms (in the high and low proportion congruent sessions, respectively) (Braver, 2012; De Pisapia and Braver, 2006). Moreover, the manipulation of congruent and incongruent Stroop trials allowed us to analyze the experienced trial-by-trial conflict. We registered participants' reports on the conscious perception of a near-threshold Gabor that was presented simultaneously to the Stroop stimulus, exploring the neural correlates of interference control and conscious perception through EEG recordings. If attention and conscious perception separately influenced decision-making concerning the perception of a stimulus, as proposed by the cumulative influence hypothesis (Tallon-Baudry, 2012), ERPs evoked by Stroop word would not differ between trials in which the near-threshold Gabor was consciously perceived as compared to trials in which the Gabor was not consciously perceived. Conversely, if attention and conscious perception interacted at the neural level, as suggested by the gateway hypothesis (Petersen and Posner, 2012; Posner, 1994), we would expect to observe differences in the ERPs evoked by the Stroop word for trials in which Gabors were consciously perceived as compared to trials in which Gabors were not consciously perceived.

The ERP results demonstrated an effect of conscious perception in the generation of the N2 component, which is assumed to reflect the operation of a conflict detection system (Luck, 2012; Yeung et al., 2004). This component demonstrated an interaction between congruency and awareness that was modulated by proportion congruency. As expected, N2 was enhanced for incongruent-seen trials as compared to incongruent-unseen trials in the high proportion congruent session. This result seems to indicate that when exerting reactive control (in the high proportion congruent condition), the detection of conflict on a given trial is associated to the conscious perception of near-threshold stimuli. In the low proportion congruency session (in which proactive control is thought to be maintained through the block), N2 was overall enhanced for seen as compared to unseen trials, although the effect was only significant for congruent trials. These results suggest that the modulation of the N2

component is related to interference control, elicited especially by incongruent trials from the high proportion congruency condition, but it is also associated to the frequency of trials in each session (the N2 modulation was more pronounced for incongruent Stroop trials from the high proportion congruent session and congruent Stroop trials from the low proportion congruent session). This observation is consistent with previous literature reporting that the N2 component is sensitive to the mismatch between an expectation and a stimulus (Luck, 2012). This expectation mismatch, which could easily be elicited by infrequent Stroop stimuli in our experimental paradigm, has also been observed to evoke ACC activity (Downar et al., 2000; Kiehl et al., 2001a, 2001b).

Source localization analyses confirmed that the ACC was one of the most activated brain regions in the time window of the N2 component. As expected, ACC activation was observed for incongruent but not for congruent trials in the high proportion congruent session (when reactive control was required), but ACC was activated for both congruent and incongruent trials in the low proportion congruent session, maybe indicating the recruitment of proactive control strategies (Braver, 2012; De Pisapia and Braver, 2006). Consistent with the ERP data, in the high proportion congruent session, ACC was activated for seen but not for unseen Gabors only for incongruent trials (in which reactive control is required). In the low proportion congruent session, ACC was activated for seen but not for unseen Gabors both for congruent and incongruent trials. This result suggests that the activation of the ACC is related both to conflict detection and the conscious perception of near-threshold information. The Global Workspace model posits the importance of frontal lobe regions in conscious perception (Baars, 2005, 2002; Dehaene et al., 2006), although evidence supporting their specific role is scarce. Our data add empirical evidence to the implication of frontal lobe functions in both interference control and conscious perception, supporting the predictions of the gateway hypothesis.

Unexpectedly, we did not observe a main effect of congruency in the N2 component. Although the type of mechanism of control recruited (reactive vs proactive control) did not modulate the N2 wave by itself, source localization analysis demonstrated that ACC activity was elicited by both congruent and incongruent Stroop trials from the low proportion congruent session. In line with these results, previous neuroimaging studies have shown that both congruent and incongruent Stroop trials can trigger higher ACC activations as compared with neutral trials (Bench et al., 1993; Carter et al., 1995). Recent studies (Goldfarb and

Henik, 2007; Kalanthroff et al., 2013; MacLeod and MacDonald, 2000) have demonstrated that Stroop tasks entangle two types of conflict: informational conflict (the conflict elicited by the relevant –word color– and the irrelevant –word meaning– dimensions of the stimuli) and task conflict (the conflict elicited by the relevant –identifying the ink color– and the irrelevant –reading the word– tasks). Although informational conflict would only be triggered by incongruent Stroop stimuli (as there is a mismatch between the information from the two dimensions of the stimulus), task conflict would be elicited by both incongruent and congruent Stroop stimuli. Therefore, task conflict could account for the activation of the ACC on congruent trials from our Stroop task.

Some authors have also tested information and task conflict in situations prompting reactive or proactive mechanisms of control (Entel et al., 2014; Kalanthroff et al., 2014, 2013). For example, Kalanthroff and colleagues demonstrated that the reduced access to proactive control mechanisms, prompted by a concurrent task of high working memory load, led to a larger task conflict (Kalanthroff et al., 2014), producing both interference (larger RTs for incongruent Stroop trials as compared with neutral Stroop trials, reflecting information conflict) and reverse facilitation (larger RTs for congruent Stroop trials as compared with neutral Stroop trials, indicative of task conflict). Thus, it is likely that our Stroop stimuli triggered both information and task conflict due to fluctuations of control strategies employed in the low proportion congruent situation (where proactive control is most likely to be elicited), and therefore recruiting ACC activation on both congruent and incongruent trials in that session. This more generalized ACC activation (affecting both congruent and incongruent trials) in the low proportion congruent condition as compared with the high proportion congruent condition could also be indicative of the use of proactive control strategies, which are thought to be maintained through the block of trials (Braver, 2012; De Pisapia and Braver, 2006).

The neural modulations described in this study could account for the observed behavioral modulation of response criterion after conflict detection in Colás et al. (2017). Contrary to our expectations, however, the results from the present study did not completely replicate our previous findings. In the previous study, we observed response criterion modulations in situations where reactive control mechanisms were more likely to be recruited (high proportion congruent session). We did not find, nor expected, modulations of conscious perception in situations where proactive control was implemented, i.e. the low proportion

congruent session. Data from the present study challenges our interpretation of the previous results, supposing that changes of response criterion were only observed in the high proportion congruent condition due to the higher amount of conflict that was triggered in incongruent trials from the high proportion congruent session, in opposition to incongruent trials from the low proportion congruent session (for a review of proportion congruent effects, see Bugg and Crump, 2012). Analyses of accuracy and RTs in the Stroop task suggest that the conflict effect in the high proportion congruent session was in fact greater than the conflict effect in the low proportion congruent session. However, in the present study the conflict-related N2 component was modulated by conscious perception in both the high and low proportion congruent sessions, indicating an expectancy-related form of conflict.

Importantly, the experimental design used in the present study varied substantially from the previous one. Specifically, in the first study we manipulated proportion congruency between participants, as opposed to the present within-participants manipulation. That is, participants from the ERP study performed both the high proportion congruent and the low proportion congruent sessions in a counterbalanced order, whereas participants from the previous study carried out only one of the mentioned sessions. Moreover, participants from the previous study also performed another less demanding session where the Gabor detection task and the Stroop task were presented in a sequential manner. Those differences could have influenced participants' preferences for reactive or proactive control mechanisms, confounding our findings by increasing individual differences in implementing different mechanisms of control (Braver, 2012; Gonthier et al., 2016) or adopting different control strategies in each study. Moreover, the previous experiment did not control for intra-individual variability in the implementation of control strategies (due to affective-motivational factors or cognitive individual differences; Braver, 2012), as it was conducted in a between-participants design. More research is needed to replicate those findings controlling for these sources of variability in order to address the necessary and sufficient conditions in which executive control impacts participants' response criterion in conscious detection tasks.

In summary, the results of the present experiment demonstrated that conscious perception is associated to an amplitude modulation of the N2 component. Therefore, the generation of a conflict related potential, known to be implicated in situations of stimuli competition or expectations' mismatch, is also associated to conscious perception of near-threshold information. If, as proposed by the cumulative influence hypothesis (Tallon-Baudry,

2012), attention independently influenced participants' perceptual decision making, we would not have expected to find differences between consciously perceived and non-perceived Gabors in a component associated to the conflict detection system, neither that this effect was modulated by our manipulations of congruency and proportion congruency.

One could argue that those differences in N2 amplitude could be related to the consequences of conscious access, such as the phenomenological experience, working memory maintenance, or metacognitive processes about the perception of the stimulus. However, it is important to consider that this effect appeared 260-360ms after the presentation of the Stroop stimulus, not after the to-be detected near-threshold Gabor. A more plausible explanation, taking into account the timing of presentation of the stimuli, is that in situations of large conflict, greater N2 component amplitudes indicate a better preparation to detect and solve the conflict, allowing the top-down amplification of information giving rise to conscious perception. This interpretation is in line with the predictions of the gateway hypothesis (Petersen and Posner, 2012; Posner, 1994) and the Global Neuronal Workspace models on consciousness (Dehaene et al., 2006, 2003; Dehaene and Changeux, 2004; Dehaene and Naccache, 2001), according to which executive attention modulates conscious perception through the top-down amplification of stimulus-evoked activity in sensory areas. Importantly, the interaction between interference control and conscious perception was associated to a neural interaction between both mechanisms in the anterior N2 component, localized in the anterior cingulate cortex.

Acknowledgements: We are grateful to the students of the University of Granada that participated in this study.

Funding: This work was supported by the Spanish Ministry of Economy and Competitiveness [research project PSI2014-58681-P to Ana B. Chica; Ramón y Cajal fellowship to Ana B. Chica, RYC-2011-09320].

References

Aru, J., Bachmann, T., Singer, W., Melloni, L., 2012. Distilling the neural correlates of consciousness. Neurosci. Biobehav. Rev. 36, 737–746. https://doi.org/10.1016/j.neubiorev.2011.12.003

Baars, B.J., 2005. Global workspace theory of consciousness: toward a cognitive neuroscience of human experience. Prog. Brain Res. 150, 45–53. https://doi.org/10.1016/S0079-6123(05)50004-9

Baars, B.J., 2002. The conscious access hypothesis : origins and recent evidence. Trends Cogn. Sci. 6, 47–52.

Bartolomeo, P., 2008. Varieties of attention and of consciousness : evidence from neuropsychology. Psyche (Stuttg). 14 (1), 1–33.

Bench, C.J., Frith, C.D., Grasby, P.M., Friston, K.J., Paulesu, E., Frackowiak, R.S.J., Dolan, R.J., 1993. Investigations of the funcitonal anatomy of attention using the Stoop test. Neuropsychologia 31, 907–922.

Botvinick, M.M., Braver, T.S., Barch, D.M., Carter, C.S., Cohen, J.D., 2001. Conflict Monitoring and Cognitive Control. Psychol. Rev. 108, 624–652. https://doi.org/10.1037//0033-295X.I08.3.624

Botvinick, M.M., Cohen, J.D., Carter, C.S., 2004. Conflict monitoring and anterior cingulate cortex: an update. Trends Cogn. Sci. 8, 539–46. https://doi.org/10.1016/j.tics.2004.10.003

Braver, T.S., 2012. The variable nature of cognitive control: a dual mechanisms framework. Trends Cogn. Sci. 16, 106–13. https://doi.org/10.1016/j.tics.2011.12.010

Bugg, J.M., Crump, M.J.C., 2012. In Support of a Distinction between Voluntary and Stimulus-Driven Control: A Review of the Literature on Proportion Congruent Effects. Front. Psychol. 3, 367. https://doi.org/10.3389/fpsyg.2012.00367

Capilla, A., Belin, P., Gross, J., 2013. The early spatio-temporal correlates and task independence of cerebral voice processing studied with MEG. Cereb. Cortex 23, 1388–1395. https://doi.org/10.1093/cercor/bhs119

Carter, C.S., Botvinick, M.M., Cohen, J.D., 1999. The contribution of the anterior cingulate cortex to executive processes in cognition. Rev. Neurosci. 10, 49–57. https://doi.org/10.1515/REVNEURO.1999.10.1.49

631 Carter, C.S., Mintun, M., Cohen, J.D., 1995. Interference and Facilitation Effects during
632 Selective Attention: An H215O PET Study of Stroop Task Performance. Neuroimage 2,
633 264–272.

634 Chica, A.B., Bartolomeo, P., 2012. Attentional routes to conscious perception. Front. Psychol.
635 3, 1. https://doi.org/10.3389/fpsyg.2012.00001

636 Chica, A.B., Bayle, D.J., Botta, F., Bartolomeo, P., Paz-Alonso, P.M., 2016. Interactions
637 between phasic alerting and consciousness in the fronto-striatal network. Sci. Rep. 6,
638 31868. https://doi.org/10.1038/srep31868

639 Chica, A.B., Botta, F., Lupiáñez, J., Bartolomeo, P., 2012. Spatial attention and conscious
640 perception: interactions and dissociations between and within endogenous and
641 exogenous processes. Neuropsychologia 50, 621–9.
642 https://doi.org/10.1016/j.neuropsychologia.2011.12.020

643 Chica, A.B., Lasaponara, S., Chanes, L., Valero-Cabré, A., Doricchi, F., Lupiáñez, J.,
644 Bartolomeo, P., 2011. Spatial attention and conscious perception: the role of endogenous
645 and exogenous orienting. Atten. Percept. Psychophys. 73, 1065–81.
646 https://doi.org/10.3758/s13414-010-0082-6

647 Chica, A.B., Paz-Alonso, P.M., Valero-Cabre, A., Bartolomeo, P., 2013. Neural Bases of the
648 Interactions between Spatial Attention and Conscious Perception. Cereb. Cortex 23,
649 1269–1279. https://doi.org/10.1093/cercor/bhs087

650 Colás, I., Triviño, M., Chica, A.B., 2017. Interference Control Modulations Over Conscious
651 Perception. Front. Psychol. 8, 1–12. https://doi.org/10.3389/fpsyg.2017.00712

652 De Graaf, T.A., Hsieh, P.J., Sack, A.T., 2012. The "correlates" in neural correlates of
653 consciousness. Neurosci. Biobehav. Rev. 36, 191–197.
654 https://doi.org/10.1016/j.neubiorev.2011.05.012

655 De Pisapia, N., Braver, T.S., 2006. A model of dual control mechanisms through anterior
656 cingulate and prefrontal cortex interactions. Neurocomputing 69, 1322–1326.
657 https://doi.org/10.1016/j.neucom.2005.12.100

658 Dehaene, S., Changeux, J., 2004. Neural Mechanisms for Access to Consciousness, in:
659 Gazzaniga, M.S. (Ed.), The Cognitive Neurosciences. The MIT Press, Cambridge, MA,
660 pp. 1145–1157. https://doi.org/10.1007/s13398-014-0173-7.2

661 Dehaene, S., Changeux, J.-P., 2011. Experimental and theoretical approaches to conscious

processing. Neuron 70, 200–27. https://doi.org/10.1016/j.neuron.2011.03.018

Dehaene, S., Changeux, J.-P., Naccache, L., Sackur, J., Sergent, C., 2006. Conscious, preconscious, and subliminal processing: a testable taxonomy. Trends Cogn. Sci. 10, 204–11. https://doi.org/10.1016/j.tics.2006.03.007

Dehaene, S., Naccache, L., 2001. Towards a cognitive neuroscience of consciousness: basic evidence and a workspace framework. Cognition 79, 1–37.

Dehaene, S., Sergent, C., Changeux, J.-P., 2003. A neuronal network model linking subjective reports and objective physiological data during conscious perception. Proc. Natl. Acad. Sci. 100, 8520–8525. https://doi.org/10.1073/pnas.1332574100

Diamond, A., 2013. Executive functions. Annu. Rev. Psychol. 64, 135–68. https://doi.org/10.1146/annurev-psych-113011-143750

Downar, J., Crawley, a P., Mikulis, D.J., Davis, K.D., 2000. A multimodal cortical network for the detection of changes in the sensory environment. Nat. Neurosci. 3, 277–283. https://doi.org/10.1038/72991

Entel, O., Tzelgov, J., Bereby-Meyer, Y., Shahar, N., 2014. Exploring relations between task conflict and informational conflict in the Stroop task. Psychol. Res. 79, 913–927. https://doi.org/10.1007/s00426-014-0630-0

Folstein, J.R., Van Petten, C., 2008. Influence of cognitive control and mismatch on the N2 component of the ERP: A review. Psychophysiology 45, 152–170. https://doi.org/10.1111/j.1469-8986.2007.00602.x

Goldfarb, L., Henik, A., 2007. Evidence for task conflict in the Stroop effect. J. Exp. Psychol. Hum. Percept. Perform. 33, 1170–1176. https://doi.org/10.1037/0096-1523.33.5.1170

Gonthier, C., Macnamara, B.N., Chow, M., Conway, A.R.A., Braver, T.S., 2016. Inducing proactive control shifts in the AX-CPT. Front. Psychol. 7. https://doi.org/10.3389/fpsyg.2016.01822

Gross, J., Kujala, J., Hamalainen, M., Timmermann, L., Schnitzler, A., Salmelin, R., 2001. Dynamic imaging of coherent sources: Studying neural interactions in the human brain. Proc. Natl. Acad. Sci. U. S. A. 98, 694–9. https://doi.org/10.1073/pnas.98.2.694

Kalanthroff, E., Avnit, A., Henik, A., Davelaar, E.J., Usher, M., 2014. Stroop proactive control and task conflict are modulated by concurrent working memory load. Psychon.

692 Bull. Rev. 22, 869–875. https://doi.org/10.3758/s13423-014-0735-x

693 Kalanthroff, E., Goldfarb, L., Usher, M., Henik, A., 2013. Stop interfering: Stroop task
694 conflict independence from informational conflict and interference. Q. J. Exp. Psychol.
695 66, 1356–1367. https://doi.org/10.1080/17470218.2012.741606

696 Kiehl, K.A., Laurens, K.R., Duty, T.L., Forster, B.B., Liddle, P.F., 2001a. Neural sources
697 involved in auditory target detection and novelty processing: an event-related fMRI
698 study. Psychophysiology 38, 133–142. https://doi.org/10.1111/1469-8986.3810133

699 Kiehl, K.A., Laurens, K.R., Duty, T.L., Forster, B.B., Liddle, P.F., 2001b. An event-related
700 fMRI study of visual and auditory oddball tasks. J. Psychophysiol. 15, 221–240.
701 https://doi.org/10.1027//0269-8803.15.4.221

702 Kusnir, F., Chica, A.B., Mitsumasu, M. a, Bartolomeo, P., 2011. Phasic auditory alerting
703 improves visual conscious perception. Conscious. Cogn. 20, 1201–10.
704 https://doi.org/10.1016/j.concog.2011.01.012

705 Luck, S.J., 2012. Event-related potentials, in: Cooper, H., Camic, P.M., Long, D.L., Panter,
706 A.T., Rindskopf, D., Sher, K.J. (Eds.), APA Handbook of Research Methods in
707 Psychology. American Psychological Association, Washington, DC, pp. 523–546.

708 MacLeod, C.M., MacDonald, P.A., 2000. Interdimensional interference in the Stroop effect:
709 Uncovering the cognitive and neural anatomy of attention. Trends Cogn. Sci. 4, 383–
710 391. https://doi.org/10.1016/S1364-6613(00)01530-8

711 Mathewson, K.E., Gratton, G., Fabiani, M., Beck, D.M., 2009. To See or Not to See: Pre-
712 stimulus Alpha Phase Predicts Visual Awareness. J. Neurosci. 29, 2725–2732.
713 https://doi.org/10.1523/JNEUROSCI.3963-08.2009

714 Oostenveld, R., Fries, P., Maris, E., Schoffelen, J.M., 2011. FieldTrip: Open source software
715 for advanced analysis of MEG, EEG, and invasive electrophysiological data. Comput.
716 Intell. Neurosci. 2011. https://doi.org/10.1155/2011/156869

717 Oostenveld, R., Stegeman, D.F., Praamstra, P., Van Oosterom, A., 2003. Brain symmetry and
718 topographic analysis of lateralized event-related potentials. Clin. Neurophysiol. 114,
719 1194–1202. https://doi.org/10.1016/S1388-2457(03)00059-2

720 Petersen, A., Petersen, A.H., Bundesen, C., Vangkilde, S., Habekost, T., 2017. The effect of
721 phasic auditory alerting on visual perception. Cognition 165, 73–81.
722 https://doi.org/10.1016/j.cognition.2017.04.004

Petersen, S.E., Posner, M.I., 2012. The attention system of the human brain: 20 years after. Annu. Rev. Neurosci. 35, 73–89. https://doi.org/10.1146/annurev-neuro-062111-150525

Posner, M.I., 1994. Attention: The mechanisms of consciousness. Proc. Natl. Acad. Sci. USA 91, 7398–7403.

Posner, M.I., Petersen, S.E., 1990. The attention system of the human brain. Ann Rev Neurosci 13, 25–42. https://doi.org/10.1146/annurev.ne.13.030190.000325

Schneider, W., Eschman, A., Zuccolotto, A., Burgess, S., Cernicky, B., Gilkey, D., Gliptis, J., Maciejczyk, V., Macwhinney, B., Rodgers, K., James, J.S., 2002. E-Prime USER'S GUIDE.

Snodgrass, J.G., Corwin, J., 1988. Pragmatics of measuring recognition memory: applications to dementia and amnesia. J. Exp. Psychol. Gen. 117, 34–50. https://doi.org/10.1037/0096-3445.117.1.34

Tallon-Baudry, C., 2012. On the neural mechanisms subserving consciousness and attention. Front. Psychol. 2, 397. https://doi.org/10.3389/fpsyg.2011.00397

Tucker, D.M., Liotti, M., Potts, G.F., Russell, G.S., Posner, M.I., 1994. Spatiotemporal analysis of brain electrical fields. Hum. Brain Mapp. 1, 134–152. https://doi.org/10.1002/hbm.460010206

Van Veen, B.D., van Drongelen, W., Yuchtman, M., Suzuki, A., 1997. Localization of brain electrical activity via linearly constrained minimum variance spatial filtering. Biomed. Eng. IEEE Trans. 44, 867–880. https://doi.org/10.1109/10.623056

Van Veen, V., Carter, C.S., 2002. The anterior cingulate as a conflict monitor: FMRI and ERP studies. Physiol. Behav. 77, 477–482. https://doi.org/10.1016/S0031-9384(02)00930-7

Wyart, V., Tallon-Baudry, C., 2009. How Ongoing Fluctuations in Human Visual Cortex Predict Perceptual Awareness: Baseline Shift versus Decision Bias. J. Neurosci. 29, 8715–8725. https://doi.org/10.1523/JNEUROSCI.0962-09.2009

Yeung, N., Botvinick, M.M., Cohen, J.D., 2004. The neural basis of error detection: conflict monitoring and the error-related negativity. Psychol. Rev. 111, 931–959. https://doi.org/10.1037/0033-295X.111.4.939